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ARENA

COMPARISON OF MESOHABSIM WITH TWO MICROHABITAT MODELS (PHABSIM AND HARPHA)

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ABSTRACT

This study demonstrates how using different habitat models can influence the results of instream habitat assessment and conclusions for river management. We used three models for a portion of the Quinebaug River (Connecticut and Massachusetts, USA): a simplistic microhabitat model with univariate habitat-use criteria and substrate-based channel index (the Physical Habitat Simulation Model (PHABSIM)); a microhabitat model using multivariate criteria including a wide range of cover attributes (HARPHA); and a mesohabitat model with multivariate habitat-suitability criteria (MesoHABSIM). The flow-habitat rating curves produced by each model were compared at two scales: site and study segment. To investigate the impact of model choice on answering questions such as which location or flow provides more habitat, we applied Spearman's correlation of ranks. The relationship between habitat-suitability predictions and fish presence at the same location was investigated with dedicated fish observations. The study showed that: (1) of the tested models, only MesoHABSIM predictions correlated with fish observations; (2) the variation within microscale models (PHABSIM and HARPHA) was greater than between micro- and mesoscale models (HARPHA and MesoHABSIM); and (3) simple univariate habitat-use criteria provided the largest source of discrepancies among the models. We suggest that these differences may lead to erroneous conclusions, especially if flow-habitat rating curve analysis is considered an endpoint of instream flow study. Copyright © 2007 John Wiley & Sons, Ltd.

KEY WORDS: MesoHABSIM; comparative study; multivariate suitability; PHABSIM; suitability criteria

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INTRODUCTION

The Physical Habitat Simulation Model (PHABSIM) was developed in the early 1970s and has become a widely accepted technique for instream habitat analysis and simulation (Bovee *et al.*, 1998; Tharme, 2003; Lamb *et al.*, 2004). It describes the hydraulic and morphological conditions in a river as an index of habitat quality obtained from observations of habitat use by a selected organism. The deterministic hydraulic model is used to calculate the changes of river hydraulics related to flow increases or decreases. The habitat-suitability index (HSI) is used to weight the wetted area of the river to describe the quantity of habitat available for a specific organism under specific conditions (i.e. flow). The output of the PHABSIM model is an input for complex flow-habitat time series analyses of stream systems proposed for significant flow alterations within the framework of Instream Flow Incremental Methodology (IFIM, Stalnaker *et al.*, 1996). The IFIM technique became very successful and created a solid tool for protecting valuable fisheries in many United States waters. Presently it is used in the US and internationally for a range of water allocation issues, and it has spawned numerous adaptations and modifications referred to as Numerical Habitat Models (NHM) (see Parasiewicz and Dunbar, 2001 for review). Over time it also inspired modified versions of the originally recommended method, without thorough review of the consequences for management decisions.

One of the PHABSIM model components frequently altered is the biological model. Within PHABSIM models some researchers use suitability criteria that consider only velocities and depth, and often only substrate size as

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driving physical attributes (e.g. Scott and Shirvell, 1987). Many criteria are also based on fish abundance histograms (utilization criteria) that include only areas occupied by fish. It should be noted that this simplified way of applying PHABSIM is not the one recommended by its creators, except for the spawning and juvenile life stages of drift feeding salmonids. More complex models incorporate a channel index, which represents cover attributes, and habitat availability (preference) as advocated by the model developers (Bovee *et al.*, 1998). Another important difference in biological models is that PHABSIM typically utilizes univariate habitat-suitability criteria, while more complex models apply multivariate statistics. In PHABSIM and follow-up models, the composite HSI is calculated variously as an average, geometric mean, product or other *a priori* selected algorithm of combining these univariate suitabilities (e.g. Pouilly and Souchon, 1995; Scruton *et al.*, 1998; Guay *et al.*, 2000, 2003). At the other end of the spectrum, artificial neuronal networks, fuzzy logic or multivariate statistics such as logistic regression are used to calculate complex indices that consider the interactive nature of multiple physical attributes (e.g. Lek *et al.*, 1996; Jorde *et al.*, 2000; Parasiewicz and Dunbar, 2001).

There are also important differences between applied hydraulic models, which range from simplified one-dimensional models to two- and three-dimensional applications (Ghanem *et al.*, 1996; Alfredsen *et al.*, 1997; Payne *et al.*, 2004). Although multidimensional hydraulic modelling has become more common in recent years, one-dimensional techniques remain the most used in the water allocation permitting process in the US. The standard-setting PHABSIM approach delineates a site into discrete cells (most frequently rectangular). The hydraulic and habitat data are collected at verticals across transects, delineating the cells. The values obtained at each vertical are assumed to represent conditions throughout the entire cell. Transect density has been widely discussed within one-dimensional hydraulic models (Simonson *et al.*, 1994; Parasiewicz, 1996). As presented by Payne *et al.* (2004), within common stand-alone applications of PHABSIM the transect spacing may range from every 10 km (6.2 mile) to less than 50 m (165 ft). The most commonly used spacing is approximately 700 m (0.42 mile) (Payne, 2004), though it frequently depends on the type of hydraulic model used. Many times transects are intended to represent the morphometry of the area for use in the step- backwater flow model (Waddle, 2001). In this case the length of cells is some proportion of the distance between transects. More appropriately, a mesohabitat-typing survey (Bovee, 1994), which determines the proportions of riffles, pools, runs, etc. within the site, precedes the cross-section measurements, and transects are used to subsample different unit types. The length of the cells is then related to the total length of hydromorphologic unit (HMU) types. The variety of applications has led to impassioned discussions of PHABSIM model validity and possible shortcomings (e.g. Mathur *et al.*, 1985; Scott and Shirvell, 1987; Gore and Nestler, 1988). The problems most commonly cited are the need for validation, the large amount of effort necessary to conduct hydrodynamic models and the associated expense (Williams, 1996; Lamb *et al.*, 2004). It was also determined that many problems arise from misapplication of the methodology (Gore and Nestler, 1988).

MesoHABSIM is a NHM that adopted the principles of PHABSIM for application at the stream-segment scale (Parasiewicz, 2001; Parasiewicz, 2007). In contrast to microscale NHMs, MesoHABSIM delineates rivers into HMUs and hydraulic attributes are measured as a quantitative distribution based on seven random measurements within each unit. The delineation is performed at a number of flows, and suitability criteria are applied to the measured data. The habitat values for flows that have not been mapped are obtained by interpolation from flow-habitat rating curves. Multivariate logistic regression is used to develop suitability criteria. Here we compare the performance of MesoHABSIM with the microhabitat models, PHABSIM and HARPHA, a more complex version of PHABSIM.

METHODS

This study used two microscale models for comparison with the MesoHABSIM prototype. First, we used a simple version of PHABSIM (as prescribed by the project contract). The model was limited to modelling summer habitat for the adult life stage of five obligatory river species during low-flow conditions. Univariate habitat-use criteria for depth, velocity and substrate were based on on-site fish observations and composite suitability (HSI) was computed as a product of suitabilities for individual attributes. A one-dimensional hydraulic model with spatially independent cross-sections was used and mesohabitat typing was employed as a basis for cross-section distribution and calculation of cell length (Bovee, 1997), and every HMU type was represented by multiple transects.

Secondly, we used the simplified HARPA model (Parasiewicz *et al.*, 1999) with the same limitations and data as above, with the following additional features—we applied preference-based suitability for depth, velocity, substrate, Froude number, undercut bank, woody debris, overhanging vegetation, submerged vegetation, boulder, riprap, canopy cover shading and shallow margin and we used a multivariate function (logistic regression) for computing probabilistic composite suitability (HPI, habitat probability index).

The model designs were chosen to reflect similar effort in data collection and computation. The field surveys for habitat data were limited to approximately 3 days of survey per site and we used data collected at the Quinebaug River (Parasiewicz, in press). All three models were created for six representative sites and used for assessment of the entire study area. Each model was developed for fallfish (*Semotilus corporalis*), common shiner (*Luxilus cornutus*), white sucker (*Catostomus commersoni*), longnose dace (*Rhinichthys cataractae*) and blacknose dace (*R. atratulus*) with flow-habitat rating curves as output. These five fluvial specialist species are the most common native fish in the Quinebaug River (Parasiewicz, in press) and therefore considered to represent the general habitat needs of the fish community. The habitat-suitability criteria were developed using the same set of on-site observations. Results are expressed as weighted useable area (WUA in m² per 1000 m). The model-specific rating curves were visually and statistically compared with one another, and the rank correlation test was conducted.

Data collection

Cross-section locations. For the simplest form of the microhabitat model, between six and 11 cross-sections were placed in each of six study sites and distributed based on the mapped mesohabitat information. Each HMU type was represented by at least four transects, although individual units could have only one transect. The average spacing between adjacent transects was 23 m (less than one river width, 76 ft). Flow-related change in the size and type of HMUs was taken into account by remapping the river at calibration flows. Three surveys were conducted to measure the hydraulic conditions at different predetermined flows, targeting conditions that would be representative of a range of flows from 0.3×10^{-2} to 3.3×10^{-2} m³ s⁻¹ km⁻² (equal to 0.3–3.0 ft³ s⁻¹ mile⁻²). During the first survey between 18 and 28 July 2001, we measured velocities with a dipping bar (Jens, 1968), depths, and substrates at each cross-section at an average flow of approximately 0.36×10^{-2} m³ s⁻¹ km⁻² (0.35 ft³ s⁻¹ mile⁻²). During the second survey from 6 to 11 August 2001, the survey team measured water surface elevation and one depth and velocity at the cross-sections at an average flow of 0.2×10^{-2} m³ s⁻¹ km⁻² (0.2 ft³ s⁻¹ mile⁻²). The same measurements were taken from 11 to 12 April 2003, at a flow of approximately 2.42×10^{-2} m³ s⁻¹ km⁻² (2.2 ft³ s⁻¹ mile⁻²).

During the first survey, the field team assessed the substrate at each vertical cell according to the choriotope classification scheme (Austrian Standard ÖNORM 6232 1995), which is composed of seven categories: pelal (<0.063 mm), psammal (0.063–2 mm), akal (2–20 mm), microlithal (20–63 mm), mesolithal (63–200 mm), macrolithal (200–400 mm) and megalithal (>400 mm). However, to allow for comparison with standard procedures used in hydraulic modelling, the study team converted each substrate measurement into a five-category classification scheme (modified Wentworth scale, Orth, 1983): sand/silt (<2 mm), gravel (2–16 mm), pebble (16–64 mm), cobble (65–256 mm) and boulder (>256 mm). The transition from seven categories to five was accomplished by combining the smallest two categories—pelal and psammal—into a single category (sand/silt) and the largest two categories—macrolithal and megalithal—into another single category (boulder). For the multivariate analysis we used the choriotope classification. Because none of the multivariate models found the merged categories significant (i.e. the models excluded them from suitability criteria), we consider the influence of this modification negligible.

Hydraulic model. One-dimensional hydraulic models were used to compute depth and velocity in the cross-section. PHABSIM uses two separate internal models for simulating the water surface elevations and mean column velocities of each cross-section at a given range of flows. The STGQ (Waddle, 2001) model was calibrated using the measured water surface elevations taken during the three hydraulic surveys. To calibrate the model, at least two measured water surface elevations were required; three were used if an additional elevation was available. After calibration, the model simulated the water surface elevations at each cross-section for a range of flows from 0.42 to 15.57 m³ s⁻¹ (15–550 cfs), in increments of 1.42 m³ s⁻¹ (50 cfs). The VELSIM velocity model with a single velocity data set was calibrated using the stage-discharge method and the mean-column velocity measurements

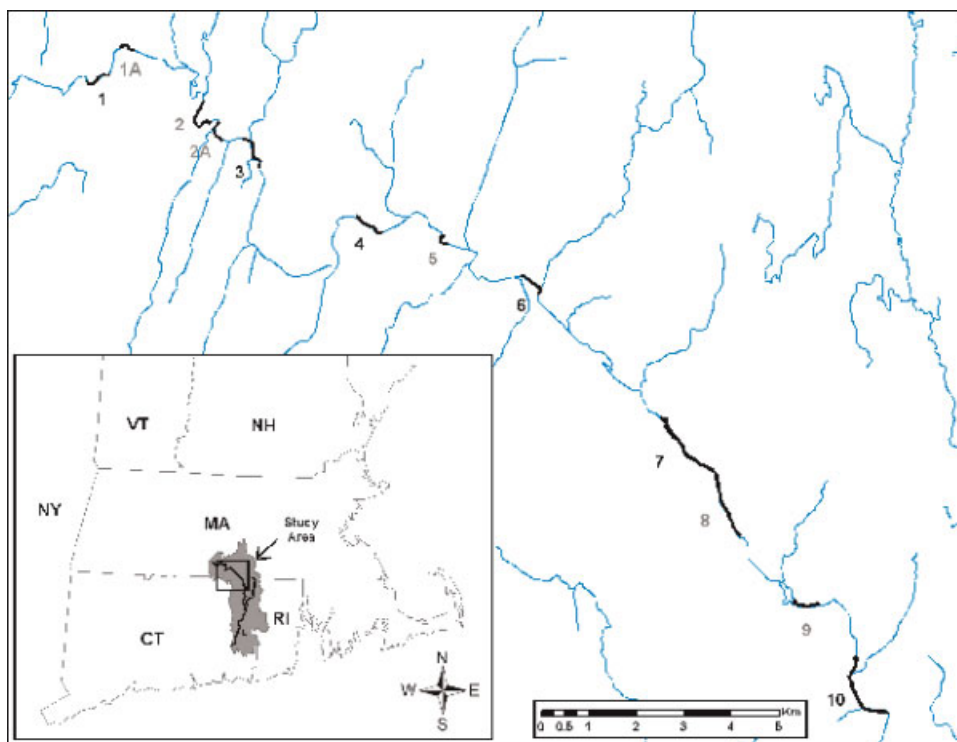


Figure 1. Map of the Quinebaug River valley study area from East Brimfield to West Thompson Lake, including location of representative sites. From 12 sites originally used in the Quinebaug Study only 6 sites, with black numbers, were used in the experiment described in this paper. Each of these sites represented specific reach (not indicated here) of the study area. This figure is available in colour online at www.interscience.wiley.com/journal/rra

taken during the medium-flow survey (Waddle, 2001). Modelled velocities and depth were verified at two other calibration flows using one sample value per cross-section.

Suitability. Two fish surveys were completed in order to develop the necessary habitat-based suitability index (SI) curves and to provide a means of evaluating the accuracy of the habitat models. The sampling sites were chosen to ensure that habitat types dominated by riffle, run, glide, backwater and pool habitats would all be represented (Figure 1). We used the pre-positioned grid technique for electrofishing as described in Bain *et al.* (1985). The first fish survey was conducted between 25 June and 17 August 2000, in six widely distributed locations on the Quinebaug River. A total of 1933 fish representing 17 species were identified from the 467 grids surveyed. The second fish survey, conducted for the purpose of model verification, was completed between 2 and 9 July 2001, at Sites 4, 7, 8 and 10. These sites were selected as having highest fish density and habitat diversity. Over 700 fish from 17 species were collected in 220 grids. The purpose of the second survey was to increase the numbers of underrepresented habitat units which could be found in these four sites.

For each species, univariate habitat-use criteria were defined for depth, velocity and substrate using data collected during the first sampling survey. Each variable was divided into a set of discrete ranges, and a SI value was assigned to each of those ranges, resulting in a continuous SI curve (Bovee *et al.*, 1998). The HSI was calculated by dividing the number of individuals of a single fish species captured in a given range of depth, velocity or substrate type by the total number of individuals of the same species caught (Figures 2–6).

The HARPMA model was developed by applying logistic regression to the microhabitat data collected at the grid samples. The model uses likelihood ratios to determine which of those parameters should be included in the following regression formula:

$$R = e^{-z}$$

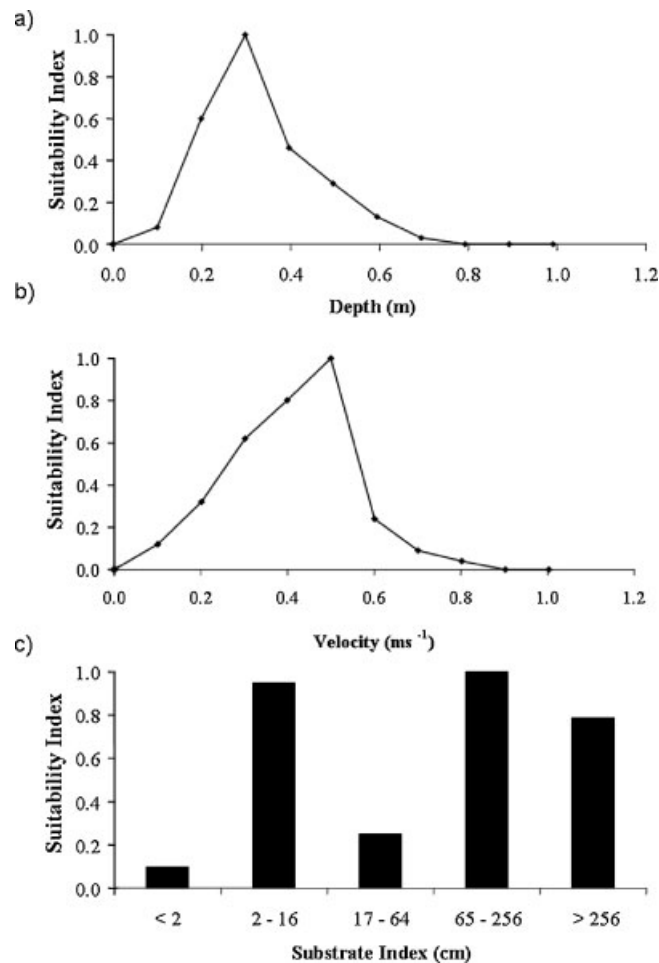


Figure 2. Univariate habitat-suitability functions for fallfish: (a) depth, (b) velocity, (c) substrate categories (as defined by dominating grain size)

where e = natural log base; $z = b_1x_1 + b_2x_2 + \dots + b_nx_n + a$; $x_{1..n}$ = significant physical variables; a = constant and $b_{1..n}$ = regression coefficients. We applied a stepwise forward logistic regression model to determine attributes that correlate well with species presence and abundance. Both regression models (presence and abundance) were used to calculate the probability of fish presence using the following equation:

$$p = \frac{1}{(1 + e^{-z})}$$

where p = probability of presence/high abundance (see Hosmer and Lemeshow, 2000 for more detail on logistic regression). In contrast with the MesoHABSIM approach, we did not include HMU classifications in the data set (Tables I and II).

Habitat model. In PHABSIM, we used the HABTAE model to predict the amount of weighted usable area (WUA) for each site at the simulated flow (Waddle, 2001). In this model the suitability indices for depth, velocity and substrate are calculated at each vertical cell and the product of all three is used to weight the cell area. For HARPHA we used the probability of fish presence and high abundance instead. The average of both probabilities is considered a composite suitability. The WUA of all cells in the site is added up into total WUA per site and standardized to 100 m length (330 ft). To define the cell length we followed the mesohabitat-typing approach described by Bovee (1994). In all the models, the WUA for fish community was calculated by summing the

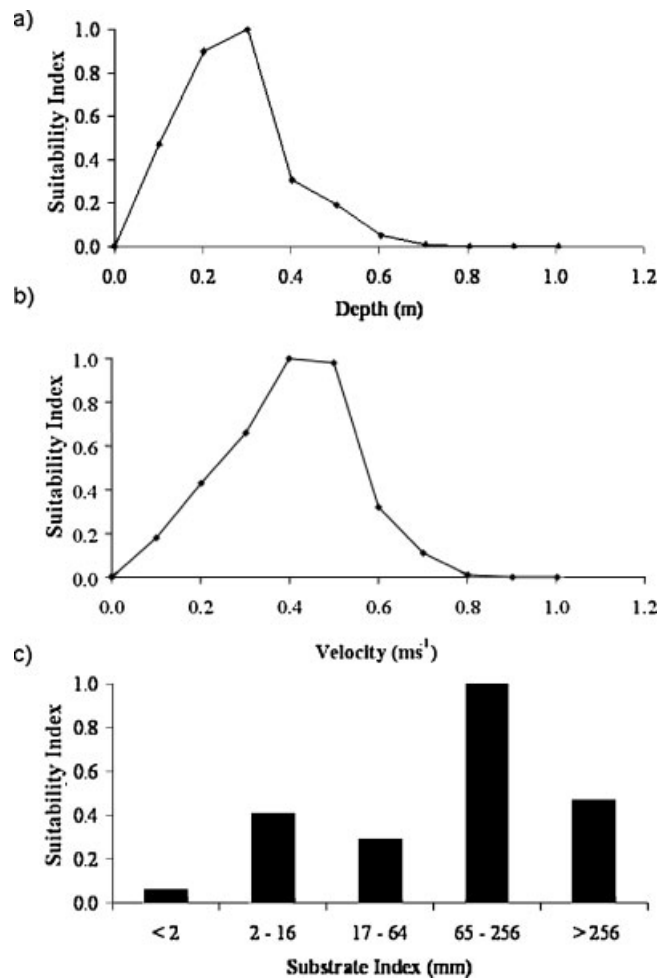


Figure 3. Univariate habitat-suitability functions for common shiner: (a) depth, (b) velocity, (c) substrate categories (as defined by dominating grain size)

species-specific WUAs weighted by species proportions expected in the target community (for values see Bain and Meixler, in press; Parasiewicz, in press). The results were used to create flow-habitat rating curves.

Testing model predictions

Model verification studies, such as the one conducted by Guay *et al.* (2000) or Thomas and Bovee (1993) can be used to confirm whether MesoHABSIM predictions reflect fish habitat use as well as a microscale NHM does. In this study the spot observations of fish density are compared to suitability indices for the same location. As argued by Williams (2001) this will still not answer with full certainty the question if the use of different models can lead to contrary conclusions. This is especially true if the process ends at a NHM and management decisions are not based on integrative IFIM procedure. To address this question, the comparative study needs to analyse the interpretation output of the models at the management scale and determine if the conclusions are similar.

The data collected during the fish surveys performed in summer 2001 were used to regress against the study model results. The flow was approximately $0.55 \times 10^{-2} \text{ m}^3 \text{ s}^{-1} \text{ km}^{-2}$ ($0.5 \text{ ft}^3 \text{ s}^{-1} \text{ mile}^{-2}$), and the location of every fishing grid was recorded and entered into a GIS model. For testing of the microhabitat model, the grids were associated with the closest cross-section. The suitabilities calculated for each cell were weighted by cell widths and

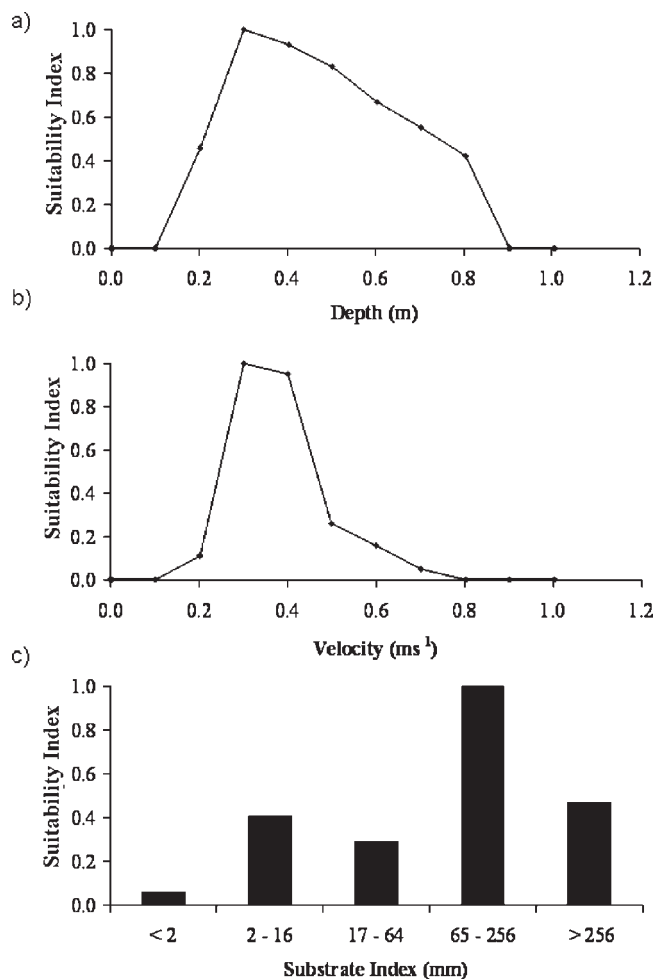


Figure 4. Univariate habitat-suitability functions for white sucker: (a) depth, (b) velocity, (c) substrate categories (as defined by dominating grain size)

averaged for each cross-section HSI or HPI. The average of HSI or HPI for the five species is compared against the number of individuals of all five species captured at the grid location. We used regression analysis to test model output versus fish numbers. In addition, we collapsed the fish density data into presence and absence of fish and categorized fished locations as unsuitable, usable and optimal as proposed by Mäki-Petäys *et al.* (2002). The cutoff values between these categories were set with an HSI of 0.2 and 0.5. Each sample was cross-classified with chi-square contingency tables as recommended by Thomas and Bovee (1993).

Comparing rating curves

To compare model output, we analysed the data at two scales: site and study area. We constructed a set of flow-habitat rating curves for each species and the community habitat at both scales. Each rating curve plotted the WUA against flow conditions from 0.3×10^{-2} to $2.2 \times 10^{-2} \text{ m}^3 \text{ s}^{-1} \text{ km}^{-2}$ (0.3 to $2.0 \text{ ft}^3 \text{ s}^{-1} \text{ mile}^{-2}$). The results of each model were then visually compared to one another to determine the effects of the different approaches on the amount of WUA and the potential analytical conclusions. For visual analysis we specifically focused on the relative position and shape of each species' curve within each site and the entire study area. In order to visually compare the rating curves, in the study area graphs we present relative WUA to the highest value obtained within each method.

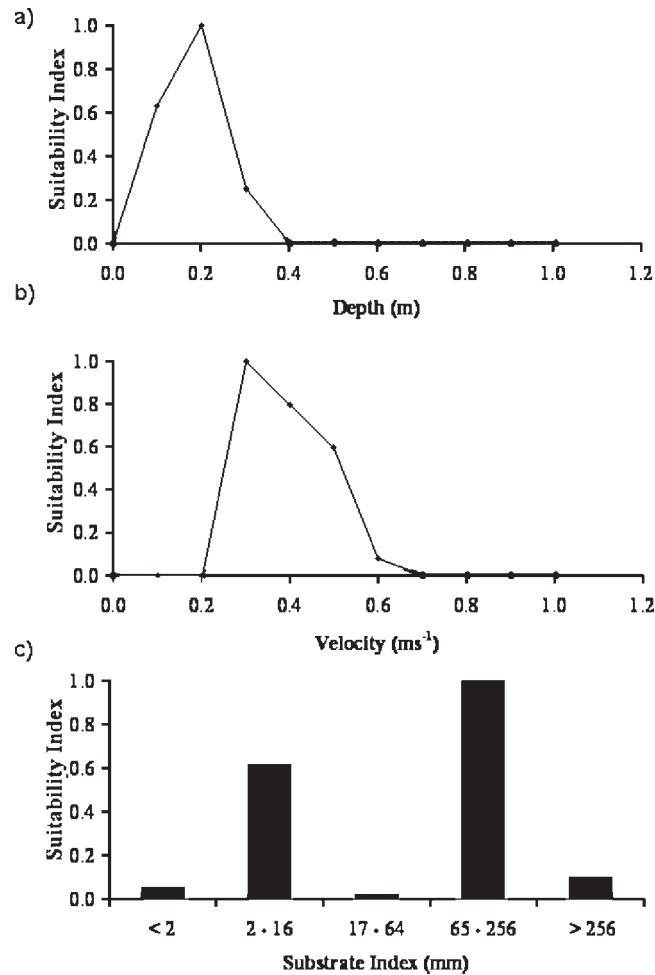


Figure 5. Univariate habitat-suitability functions for blacknose dace: (a) depth, (b) velocity, (c) substrate categories (as defined by dominating grain size)

To visualize the changes in magnitude between the methods and the sites, at the site scale y-axis is displayed in the absolute numbers with the method specific maximum value.

As previously stated, our objective was to determine if the choice of model could substantially influence the interpretation of results. For statistical analysis we formulated key questions to be answered during typical interpretation: Which site has the greatest amount of suitable habitat? At what flow are the highest amounts found? What species has the maximum habitat and where? These questions are addressed by analysing the ranking of species-specific habitats in sites and study area in terms of quantity. We used Spearman rank correlations on WUAs (Kendall and Dickinson Gibbons, 1990) to analyse species-specific WUAs calculated for each site and study area at four flows: 0.33×10^{-2} , 0.66×10^{-2} , 1.1×10^{-2} and $2.2 \times 10^{-2} \text{ m}^3 \text{ s}^{-1} \text{ km}^{-2}$ (0.3 , 0.6 , 1.0 and $2.0 \text{ ft}^3 \text{ s}^{-1} \text{ mile}^{-2}$). These flows were the closest to those mapped within MesoHABSIM. For comparison at the study area scale we used WUAs at six interpolated flow conditions 0.33×10^{-2} , 0.55×10^{-2} , 0.77×10^{-2} , 1.1×10^{-2} , 1.7×10^{-2} and $2.2 \times 10^{-2} \text{ m}^3 \text{ s}^{-1} \text{ km}^{-2}$ (0.3 , 0.5 , 0.7 , 1.0 , 1.5 and $2.0 \text{ ft}^3 \text{ s}^{-1} \text{ mile}^{-2}$). To determine which site provided the maximum habitat for a species, we ranked the sites by their suitability for individual species based on predicted WUA magnitude (we call this Site for Species Ranking). To determine which species had the maximum habitat at a location we ranked species within each site based on the amount of habitat available to them (Species at Site Ranking). To analyse how models answer the question of which flow is best for the species at a site, we sorted data

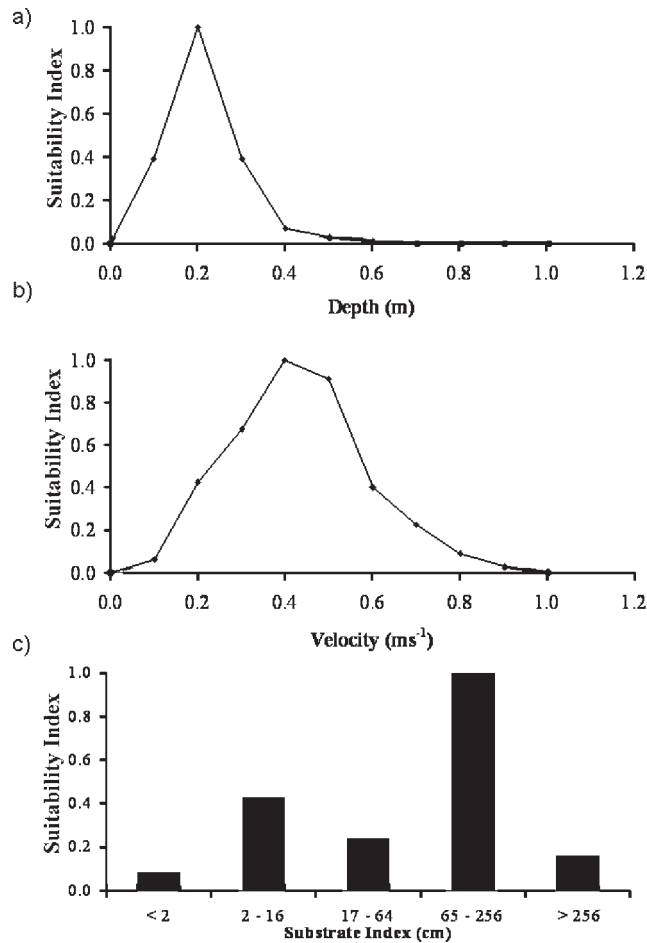


Figure 6. Univariate habitat suitability functions for longnose dace: (a) depth, (b) velocity, (c) substrate categories (as defined by dominating grain size)

by species and sites and ranked the flows accordingly (Flow Ranking). This was done to avoid potential autocorrelations caused by species or site dependences of WUA. At the study area scale we asked the same questions by ranking the species and flows.

RESULTS

Regression analysis

In the 220 grids sampled during the 2001 fishing survey at Sites 4, 7 and 10, the study team collected 180 adult fish, 100 of which were fallfish. Most of the adult fish (122) were found at Site 4. An additional 606 fish were captured during the survey; however, they were young-of-the-year and were not used for validation of the rating curves. Only 179 grids were within the same units as cross-sections. Within these grids, the team captured 166 adult fish, 92 of which were fallfish.

The MesoHABSIM approach is the only investigated method that shows a significant regression between predicted probabilities of fish presence and the numbers of fish caught in the area (Figure 7). The R^2 value is relatively low (0.22), but nevertheless significant ($p=0.00$). These results are consistent with chi-square contingency table analysis, which confirmed highly significant separation of fish occupancy for MesoHABSIM only ($p=0.00$).

Table I. The logistic regression-based suitability coefficients for selected target species developed for the microhabitat model (HARPHA)

Fallfish	Common shiner		White sucker		Longnose dace		Blacknose dace	
	Presence (75%)	<i>b</i>	Presence (80%)	<i>b</i>	Presence (95%)	<i>b</i>	Presence (92%)	<i>b</i>
Submerged vegetation		-0.81		1.71		5.01		-1.17
Boulder		1.80	Boulder	1.4	Depth (50–100 cm)	2.19	Overhanging vegetation	2.02
Shading		-0.98	Riprap	-1.48	Depth (50–75 cm)	1.62	Riprap	1.38
Depth (0–25 cm)		-1.46	Shading	-1.23	Mesolithal	1.66	Depth (0–25 cm)	2.51
Velocity (45–60 cm s ⁻¹)		1.29	Depth (50–75 cm)		Undercut bank		Velocity (75–90 cm s ⁻¹)	
Microlithal		-1.83						
Mesolithal		-0.92						
High abundance (60%)	<i>b</i>		High abundance (69%)	<i>b</i>	High abundance (66%)	<i>b</i>	High abundance (73%)	<i>b</i>
Overhanging vegetation	-1.01		Boulder	1.68	Depth (75–100 cm)	7.62	Velocity (45–60 cm s ⁻¹)	3.35
			Shading	-1.01			Microlithal	-4.2

The table shows two models for each species, one for presence and one for high abundance. The *b* coefficients are multipliers of the significant attribute values. The number in parentheses is the predictive power of the model obtained from classification tables.

Table II. The logistic regression-based suitability coefficients for selected target species used in MesoHABSIM

Fallfish	Common shiner		White sucker		Longnose dace		Blacknose dace		
Presence (76%)	<i>b</i>	Presence (80%)	<i>b</i>	Presence (95%)	<i>b</i>	Presence (92%)	<i>b</i>	Presence (94%)	<i>b</i>
Boulder	1.95	Boulder	1.71	Depth (75–100 cm)	5.01	Riffle	2.05	Depth (0–25 cm)	3.03
Shading	–1.07	Riprap	1.4	Depth (50–75 cm)	2.19	Fast run	2.45	Boulder	2.57
Depth (0–25 cm)	–1.76	Shading	–1.48	Mesolithal	1.62	Xylal	4.6	Shading	–1.44
Velocity (45–60 cm s ^{–1})	1.06	Depth (50–75 cm)	–1.23	Undercut bank	1.66	Riprap	2.29	Shallow margin	1.65
Run	–0.57							Pelal	3.09
								Velocity (45–60 cm s ^{–1})	1.46
								Submerged vegetation	–1.44
High abundance (60%)	<i>b</i>	High abundance (69%)	<i>b</i>	High abundance (66%)	<i>b</i>	High abundance (73%)	<i>b</i>	High abundance (79%)	<i>b</i>
Overhanging vegetation	–0.97	Boulder Shading	1.68 –1.01	Depth (75–100 cm)	7.62	Velocity (45–60 cm s ^{–1})	3.35	Microlithal	–4.2

The table displays two models for each species, one for presence and one for high abundance. The *b* coefficients are multipliers of the significant attribute values. The number in parentheses defines the predictive power of the model.

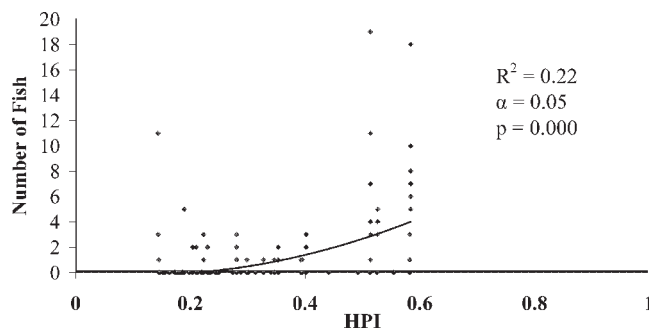


Figure 7. Regression analysis for MesoHABSIM model. The *x*-axis represents the average suitabilities calculated for specific grid location, and the *y*-axis is the number of individual fish captured there

Rating curves interpretation

Variation within microscale models. Table III summarizes rank correlation coefficients computed for each model comparison. The individual results will be presented in appropriate sections below.

At the study-segment scale (after extrapolation from representative sites) both microhabitat models (PHABSIM and HARPHA) differ in the shapes of their rating curves (Figure 8a and b). No meaningful positive rank correlation could be documented for any of the investigated interpretations. The PHABSIM model rating curves are bell-shaped, showing the most available habitat for white sucker, common shiner and fallfish. While the later two species have relatively steady rating curves with peaks around $0.55 \times 10^{-2} \text{ m}^3 \text{ s}^{-1} \text{ km}^{-2}$ ($0.5 \text{ ft}^3 \text{ s}^{-1} \text{ mile}^{-2}$), white sucker habitat shows a strong and steady increase up to a flow of $1.65 \times 10^{-2} \text{ m}^3 \text{ s}^{-1} \text{ km}^{-2}$ ($1.5 \text{ ft}^3 \text{ s}^{-1} \text{ mile}^{-2}$). Blacknose dace and longnose dace show similar amounts of habitat at the lower flow spectrum. The community curve is low, with an inflection point at $0.55 \times 10^{-2} \text{ m}^3 \text{ s}^{-1} \text{ km}^{-2}$ ($0.5 \text{ ft}^3 \text{ s}^{-1} \text{ mile}^{-2}$). In absolute values of WUA the HARPHA model compared to the PHABSIM model indicate more available habitat by almost a factor of 10. The

Table III. Coefficients of Spearman's rank correlations between the results of different models

	PHABSIM	HARPHA	MesoHABSIM
Site scale			
Sites ranked by WUA for species			
PHABSIM	1.00	0.07	0.05
HARPHA	0.07	1.00	0.37
MesoHABSIM	0.05	0.37	1.00
Species ranked by WUA in the sites			
PHABSIM	1.00	-0.35	-0.05
HARPHA	-0.35	1.00	0.42
MesoHABSIM	-0.05	0.42	1.00
Flows ranked by WUA in the sites for species			
PHABSIM	1.00	-0.17	0.01
HARPHA	-0.17	1.00	0.07
MesoHABSIM	0.01	0.07	1.00
Study area scale			
Species ranked by WUA			
PHABSIM	1.00	-0.47	-0.43
HARPHA	-0.47	1.00	0.97
MesoHABSIM	-0.43	0.97	1.00
Flows ranked by WUA for species			
PHABSIM	1.00	-0.02	0.23
HARPHA	-0.02	1.00	0.22
MesoHABSIM	0.23	0.22	1.00

The numbers in bold are significant for $p < 0.01$.

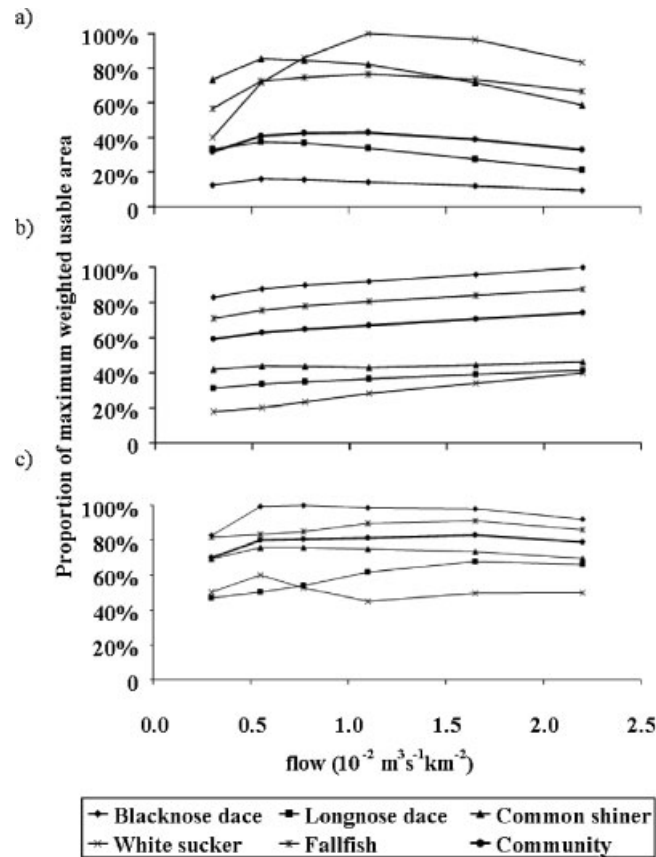


Figure 8. Habitat versus flow rating curves calculated for the study-segment scale with three different models: (a) PHABSIM, (b) HARPFA, (c) MesoHABSIM

rating curves increase steadily, with slight inflection points around $0.55 \times 10^{-2} \text{ m}^3 \text{ s}^{-1} \text{ km}^{-2}$ ($0.5 \text{ ft}^3 \text{ s}^{-1} \text{ mile}^{-2}$). Blacknose dace has the most available habitat, followed by fallfish. Common shiner and longnose dace have approximately half as much habitat as the two former species. White sucker has the least amount of habitat.

At the site scale, the results of the PHABSIM model are sometimes counter-intuitive. For simplicity here we point only to the most curious results (Figures 9a–14a). According to this model, Site 6 has the most available habitat overall. Yet this site shows clear signs of channelization and would not be expected to contain desirable habitat. This was also supported by our fishing surveys showing low fish density. Sites 3 and 10 show almost no habitat, which does not seem to be correct, at least with regard to Site 10, because of the relatively good morphological character of this site.

The results of the HARPFA match better our professional judgment (Figures 9b–14b). All sites show similar levels of suitable habitat, with the exception that quantities at Sites 1 and 3 are lower. Site 7 is the most sensitive to flow changes. Compared with PHABSIM the greatest discrepancy is the distribution of habitat among the species in sites. This is confirmed by significant negative correlations of Species at Sites Ranks (Table III).

Use of microhabitat versus mesohabitat scales. The results of MesoHABSIM are more consistent with the HARPFA model. Therefore, our analysis of the discrepancies caused by use of meso versus microhabitat model will focus on two models only: MesoHABSIM and HARPFA.

At the study-segment level the order of species in rating curves is very similar for MesoHABSIM and HARPFA models, but their shapes are different (Figure 8). This is confirmed by Spearman's rank correlations that are high and significant for Species at Site Ranking ($r = 0.97$, $p < 0.01$) and non-existent for ranking flows (Table III). From a shape perspective, the MesoHABSIM curves are less steady and have shallower slopes than in the HARPFA

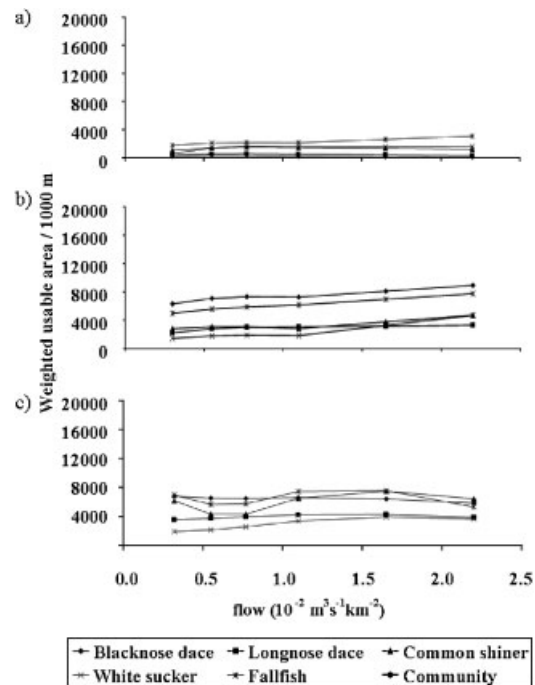


Figure 9. Habitat versus flow rating curves calculated for the representative Site 1: (a) PHABSIM, (b) HARPHA, (c) MesoHABSIM

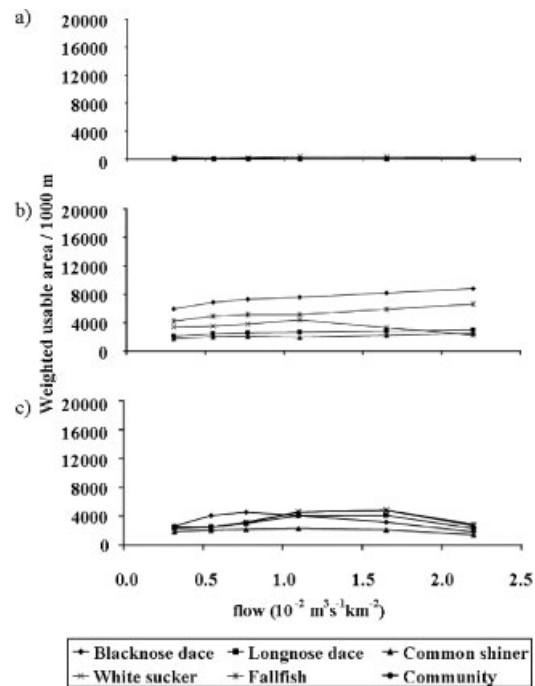


Figure 10. Habitat versus flow rating curves calculated for the representative Site 3: (a) PHABSIM, (b) HARPHA, (c) MesoHABSIM

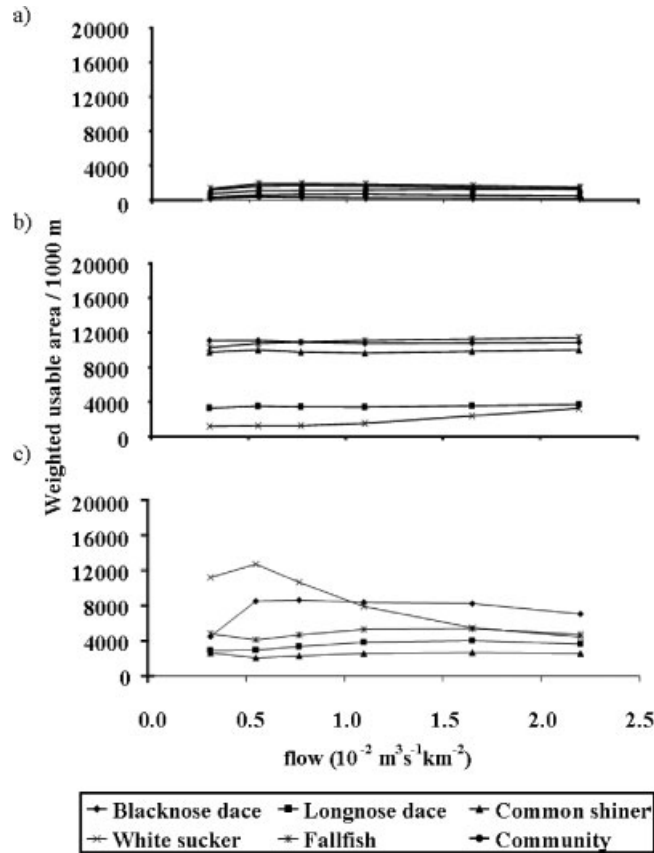


Figure 11. Habitat versus flow rating curves calculated for the representative Site 4: (a) PHABSIM, (b) HARPHA, (c) MesoHABSIM

model. The shapes of the MesoHABSIM rating curves are also less uniform, indicating that the MesoHABSIM model may be more sensitive to flow changes than HARPHA. When compared to PHABSIM no correlation with MesoHABSIM results could be observed.

At the site scale, the differences between MesoHABSIM and HARPHA are more prominent, with very poor correlations for all interpretations (Figures 9–14). However, both models indicate that Site 7 has the highest amount of habitat followed by Sites 10 and 6. Sites 3 and 4 have lower habitat levels in the MesoHABSIM. Both models predict similar habitat levels for Sites 1 and 3.

The comparison of rating curves of MesoHABSIM and PHABSIM gives almost identical results as the comparison of HARPHA and PHABSIM. The greatest discrepancies are in evaluation of Sites 10 and 6 and in Species at Site Rankings.

DISCUSSION

It must be noted that the PHABSIM application used in this study violates protocols recommended by the creators of the model in two ways. First, although transect spacing is more dense than in 98% of studies reported in Payne *et al.* (2004), it is insufficient to characterize the highly heterogenous configuration of habitats in the Quinebaug River. Secondly, utilization suitability curves were used instead of preferences, and habitat characteristics were limited to depth, velocity and substrate in the PHABSIM application. Similarly, the MesoHABSIM model used a mix of microscale criteria (depth, velocity and substrate) with mesoscale characteristics of HMUs, creating inconsistency of scale.

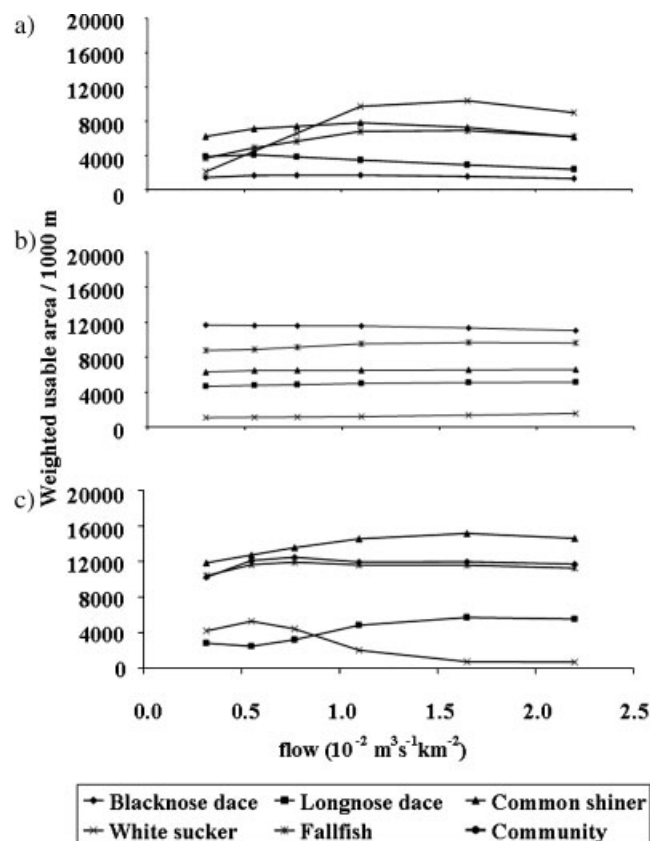


Figure 12. Habitat versus flow rating curves calculated for the representative Site: (a) PHABSIM, (b) HARPHA, (c) MesoHABSIM

Only recently have validation and comparative studies between various models become common in the literature (Boudreau *et al.*, 1996; Scruton *et al.*, 1998; Guay *et al.*, 2000, 2003; Harby *et al.*, 2005). Some validation studies conducted at the site scale could not document a positive relationship between WUA and fish densities (Scott and Shirvell, 1987; Bourgeois *et al.*, 1996) while others could show evidence to the contrary (Orth and Maughan, 1982; Bovee *et al.*, 1994, 1998; Boudreau *et al.*, 1996; Guay *et al.*, 2000, 2003). These discrepancies are frequently attributed to the variety of models used in these studies (Scruton *et al.*, 1998; Guay *et al.*, 2000, 2003). We are not aware of a comprehensive study that compares the outcomes of all core models and their corollaries and validates all sources of variation. Neither does this study provide such a comprehensive view mainly because of available resources and limitation of the overall objectives of the river restoration project. Therefore, the results should not be considered a full comparison of the two types of techniques, but understood as representing three specific models constrained by the described limitations and tested within the altered environment of the Quinebaug River. Nevertheless, the findings of this project provide valuable insight into model performance.

Although the MesoHABSIM model shows a significant correlation between predicted habitat levels and number of fish caught, the relationship is much weaker than that observed by Guay *et al.* (2000) and shows considerable variance. One of the reasons may be that the fauna of the Quinebaug River are affected by low flows, high summer temperatures and limited proportions of good habitat conditions. The fish density is low and the habitat is not fully utilized. Furthermore, in contrast to the study by Guay *et al.* (2000), our work did not focus on a single species but on the five most common species of the fish community, for which behavioural cues may not be as clear as for the cited study's juvenile salmon. Fish are mobile animals and even during intensive surveys, researchers can only capture a snapshot of fish behaviour. It is also well known that fish show diurnal habitat-use patterns, which were not incorporated into these models. Finally, as suggested by Cade and Noon (2003), the habitat models encompass only

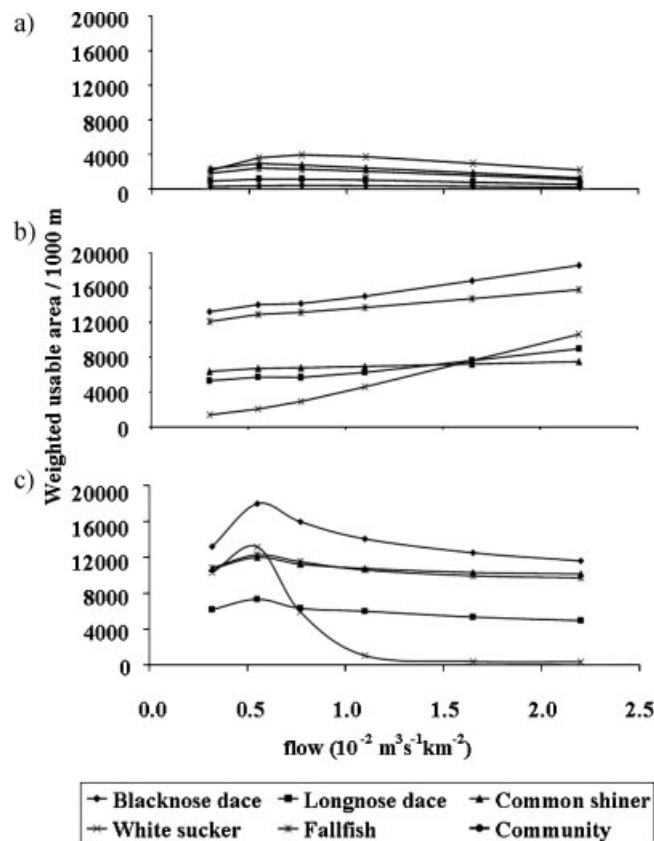


Figure 13. Habitat versus flow rating curves calculated for the representative Site 7: (a) PHABSIM, (b) HARPHA, (c) MesoHABSIM

a portion of factors influencing fish behaviour. Use of quantile regression as proposed by the same authors is likely to be a more precise method than methods applied here. The fact that despite all these factors the correlations between model output and fish density could be established is encouraging. It obviously does not replace the ultimate test, conducted on multiple rivers with a lower level of impact. Such a test is presently underway at the University of Connecticut.

Unsuccessful validation of PHABSIM and HARPHA may be caused by low density of sampled cross-sections. Although within a representative site the transects are spaced much more densely than in most of the applied PHABSIM studies (Payne, 2004), extrapolating the hydraulic model to longer river sections still increases the second stage error. It is conceivable that after investing much more effort in data collection the results of model validation studies could be successful. Our test was designed to compare models created with similar effort, and this could be controlled only by lowering the transect density. Although the field data collections for microscale NHMs were less intensive than for MesoHABSIM, the computations were very time-consuming, particularly for PHABSIM.

The comparative tests for PHABSIM and HARPHA suggest that the PHABSIM model suffers from simplistic suitability criteria (univariate use curves without incorporating channel index). For experts familiar with the river, the ranking of the sites with regard to habitat quantity by univariate PHABSIM was illogical (e.g. Sites 4 and 7) and contrary to our observations of fish abundances in these sites.

Another observation is that the variability in habitat ranking can be greater within microscale models than between micro- and mesoscale models due to the wide range of habitat components, HSI and quality of habitat sampling. The results of the HARPHA and MesoHABSIM models are consistently more similar than HARPHA and PHABSIM. Using either model would lead to the determination of the same sites as good or poor and similarly

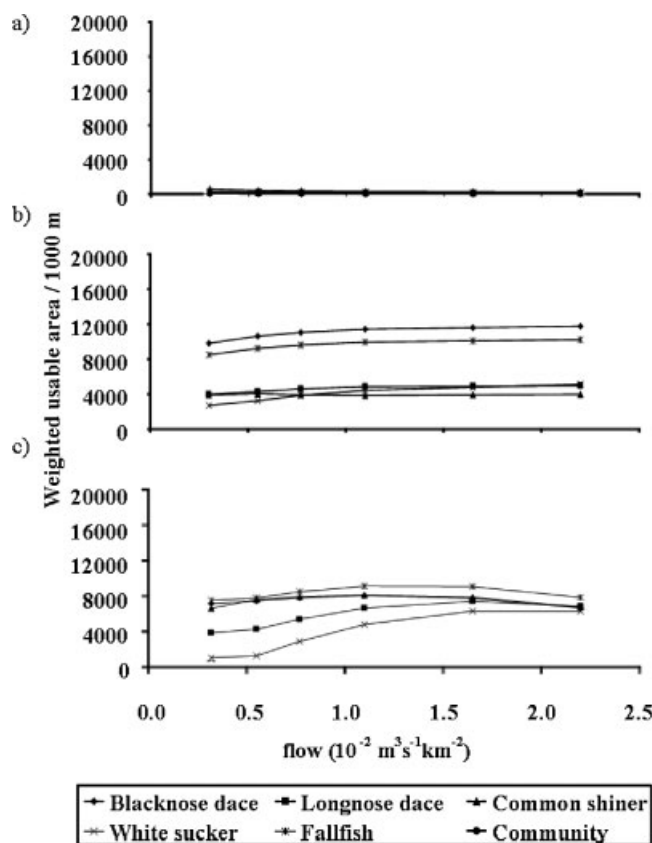


Figure 14. Habitat versus flow rating curves calculated for the representative Site 10: (a) PHABSIM, (b) HARPHA, (c) MesoHABSIM

evaluate which species have the most suitable habitat available. However, they are not consistent with regard to qualification of suitability of different flows. These differences are also not consistent among the species. The largest incongruence is in habitat availability for common shiner and white sucker. In both cases the biological model suffered from low numbers of observations of these species. The above is true regardless of whether the analytical scale is based on representative site or study area.

The rank correlation analysis and visual comparison of flow-habitat rating curves indicate that there are significant differences among the outputs of all three models. These differences could lead to varying conclusions about the magnitude of available habitat, the inflection points of rating curves, the habitat stability, the species-habitat dominance structure and the relative suitability of specific sites. For example with PHABSIM, Sites 4, 7 and 10 would be classified as having very poor habitat; HARPHA and MesoHABSIM would make the opposite determination. The biggest differences among the models occur when ranking habitat among species (e.g. Site 1).

We make the major conclusion that the placement of transects and the inclusion of cover in the microhabitat model likely have a great influence on study results and subsequent decisions. This is most probable if analysis of rating curves becomes the endpoint for subjective impact assessment, and models do not undergo the scrutiny of the full IFIM procedure by demonstrating that the underlying assumptions are met. The more simplistic approach that uses few transects and ignores instream and overhead cover is being used in the regulatory practice of instream flow determination. This is unfortunate because the quality of the biological model (i.e. development and testing of suitability criteria) may have a stronger influence on modelling results than the spatial resolution of the hydraulic component of the model. Therefore, we postulate here that this aspect should be given particular attention when applying any physical habitat model.

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